


Applying network theory to animal movements to identify properties of landscape space use

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Abstract. Network (graph) theory is a popular analytical framework to characterize the structure and dynamics among discrete objects and is particularly effective at identifying critical hubs and patterns of connectivity. The identification of such attributes is a fundamental objective of animal movement research, yet network theory has rarely been applied directly to animal relocation data. We develop an approach that allows the analysis of movement data using network theory by defining occupied pixels as nodes and connection among these pixels as edges. We first quantify node-level (local) metrics and graph-level (system) metrics on simulated movement trajectories to assess the ability of these metrics to pull out known properties in movement paths. We then apply our framework to empirical data from African elephants (*Loxodonta africana*), giant Galapagos tortoises (*Chelonoidis* spp.), and mule deer (*Odocoileus hemionus*). Our results indicate that certain node-level metrics, namely degree, weight, and betweenness, perform well in capturing local patterns of space use, such as the definition of core areas and paths used for inter-patch movement. These metrics were generally applicable across data sets, indicating their robustness to assumptions structuring analysis or strategies of movement. Other metrics capture local patterns effectively, but were sensitive to specified graph properties, indicating case specific applications. Our analysis indicates that graph-level metrics are unlikely to outperform other approaches for the categorization of general movement strategies (central place foraging, migration, nomadism). By identifying critical nodes, our approach provides a robust quantitative framework to identify local properties of space use that can be used to evaluate the effect of the loss of specific nodes on range wide connectivity. Our network approach is intuitive, and can be implemented across imperfectly sampled or large-scale data sets efficiently, providing a framework for conservationists to analyze movement data. Functions created for the analyses are available within the R package moveNT.

Key words: animal movement; connectivity; GPS radio telemetry; movement corridor; network (graph) theory; space use.

INTRODUCTION

The field of movement ecology has expanded rapidly in recent years due to advances in spatiotemporal data collection (facilitated by innovations in tracking technology; Kays et al. 2015) and the coordinated development of new analytical approaches (Börger 2016). These advances have provided insight to fundamental questions on animal behavior and individual–landscape interactions (e.g., Avgar et al. 2015, Basille et al. 2015, Bastille-Rousseau et al. 2015, Potts and Lewis 2016). Despite the many opportunities created by improvements on these two fronts, there is an emerging disconnect between the development of sophisticated analytical approaches and applications to behavioral and applied questions (Börger 2016). This disconnect is caused by complexity in analytical approaches, associated computational limitations when implementing them to large data sets, and a lack of compiled tools and functions to make methods accessible

to general ecologists. In this context, approaches that are intuitive, accessible and implementable for large-scale and often imperfectly sampled data sets are desirable.

In network theory (or graph theory), the structural aspects (i.e., configuration) of a set of nodes (also called vertices or points) and their connections (edges) can be quantified using a diversity of metrics that characterize the position and significance of nodes to the overall graph structure and integrity. As a simple example, air transportation can be seen as a network where nodes are represented by the different airports, edges represented as connections among airports, and network metrics can be calculated to help identify critical hubs in the network. Overall, network theory is a popular analytical framework for characterizing the structure and dynamics of node-based data that has been applied to system analyses in a wide variety of sciences including ecology, physics, computer science, economics, and sociology (Watts and Strogatz 1998). The ability to pinpoint critical hubs and connections structuring a network and its dynamics has made these approaches instrumental in relating processes and patterns. Relevant to movement, network theory is commonly applied in the assessments of human transportation and infrastructure networks (Guimerà et al.

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2005, Kurant and Thiran 2006). In animal ecology, application of network theory has been more commonly applied to the study of population rather than spatial processes, including wildlife epidemiology (Keeling and Eames 2005), social systems, and the interaction structure among individuals (Croft et al. 2011, Pinter-Wollman et al. 2014), and food webs (Dunne et al. 2002). But application of network theory to spatial processes in ecology is growing.

Network theory is increasingly being adopted in landscape ecological approaches to quantify connectivity within landscape, where patches of suitable habitats are represented as nodes, and connectivity among specific patches as undirected edges (Minor and Urban 2008, Galpern et al. 2011). Applications of network theory in this context have helped identify critical areas for the protection of endangered species (Fortuna et al. 2006, O'Brien et al. 2006) as well as consequences of human interventions on predator-prey interactions (Courbin et al. 2014). More recently, network theory has been applied to look at sequential locational use through analysis of data from arrays (point survey locations) acquired from acoustic telemetry or mark-recapture to quantify animal movement based connectivity (Desender et al. 2006, Finn et al. 2010, Fletcher et al. 2011, Jacoby et al. 2012, Stehfest et al. 2013, 2015, Fox and Bellwood 2014, De Lima et al. 2015, Papastamatiou et al. 2015). Despite the richness of satellite tracking data being collected on numerous species globally (Kays et al. 2015), network theory has rarely been applied directly to actual relocation movement (i.e., satellite telemetry) data. Where it has been applied, it has served to highlight properties of spatially restricted behaviors like resting locations (Fortuna et al. 2009, Wittemyer et al. 2017). Expanding its application can serve to define emergent properties regarding the organizational structure of animal space use in a manner that is less restrictive and sensitive to a priori definitions of behavioral categorization or spatial definitions of locations (e.g., node, edges, and landscape characteristics).

Combining network theory with movement data provides a promising approach for the analysis of relocation data (reviewed in Jacoby and Freeman 2016). Network theory relies on a mathematical framework that allows the calculations of metrics that can be extracted at the node-, edge-, or graph-levels (Rayfield et al. 2011). Node centrality metrics, like weight and degree, can serve to identify areas of exceptional use (potential importance). Metrics of betweenness (e.g., betweenness centrality) can provide insight to nodes critical for connectivity in a system, while metrics that define communities (e.g., clustering coefficient) can illuminate spatial structuring (i.e., neighborhoods). Furthermore, metrics can identify the time-specific directionality of movements and the degree of flow across the system. These measures may have an intuitive appeal to movement ecologists given the intrinsic similarity in properties captured by network metrics with some of the common goals of animal movement studies (Jacoby and Freeman 2016). Most useful may be defining animal core range and locations important to flow and connectivity in a landscape (i.e., corridors). Yet, application of network theory to relocation data acquired from GPS telemetry remains rare.

Our goal here is to develop an intuitive approach for translating animal movement data acquired from relocation

data into a network framework, and then investigate the potential of network theory as a suite of analytical tools for relocation data. Initially, we demonstrate an approach for developing a movement-based network for analysis of relocation data that can quickly produce a visually rich summary of animal movement properties. We then test the potential of network theory for two applications, namely (1) the utility of node-level metrics to reveal local properties of animal movement and (2) the use of graph-level metrics to characterize movement patterns. We explore these objectives on simulated movement data with known characteristics and then apply our analytical framework to empirical data from African elephants (*Loxodonta africana*), giant Galapagos tortoises (*Chelonoidis* spp.), and mule deer (*Odocoileus hemionus*) to illustrate applications of our approach to empirical animal movement data. We discuss the potential of our approach to advance movement analysis and interpretation of space use behavior, highlighting the utility of different metrics for different objectives and scales of analyses.

METHODS

From movement relocations to a movement network

To translate movement into a format that can be analyzed using graph theoretic approaches, we overlaid relocation data on a grid (i.e., rasterized the data), where each pixel represented a separate node (Fig. 1, first row). Movement from one pixel to another was represented by an edge, and the edge was weighted by the number of times this transition was observed. Because connections between nodes summarized in this manner are a function of the GPS data collection resolution and the pixel size, we defined pixel size based on the emergent step length distribution as the median inter-point distance (i.e., median step length) for a given individual. We tested the sensitivity of various metrics to the defined grid resolution (discussed in the “Node-level metrics and local space-use” section). From this discretization of the movement data, we can derive the adjacency matrix of the graph. The adjacency matrix contains the counts of transitions between any two cells of the grid. Depending on the question of interest, we can generate an adjacency matrix that is unweighted (i.e., with binary elements rather than counts), directed (i.e., where the direction of transitions matters), and representing individual- or population- (all sampled individuals in combination) level movements.

The adjacency matrix can be used for the calculation of numerous network metrics (Fig. 1, Table 1), offering inference at the node (local) or graph (system) level. Node-based metrics can also be subsequently summarized at the graph level (e.g., by calculating averages, coefficient of variation, spatial autocorrelation, etc.). We employed the metrics available within the package *igraph*, a package (available in R, python and C) providing efficient network analytics, and summarized the definitions of these metrics in Table 1 (*igraph available online*).⁷ We calculated the metrics using the weighted adjacency matrices when required.

⁷ www.igraph.org

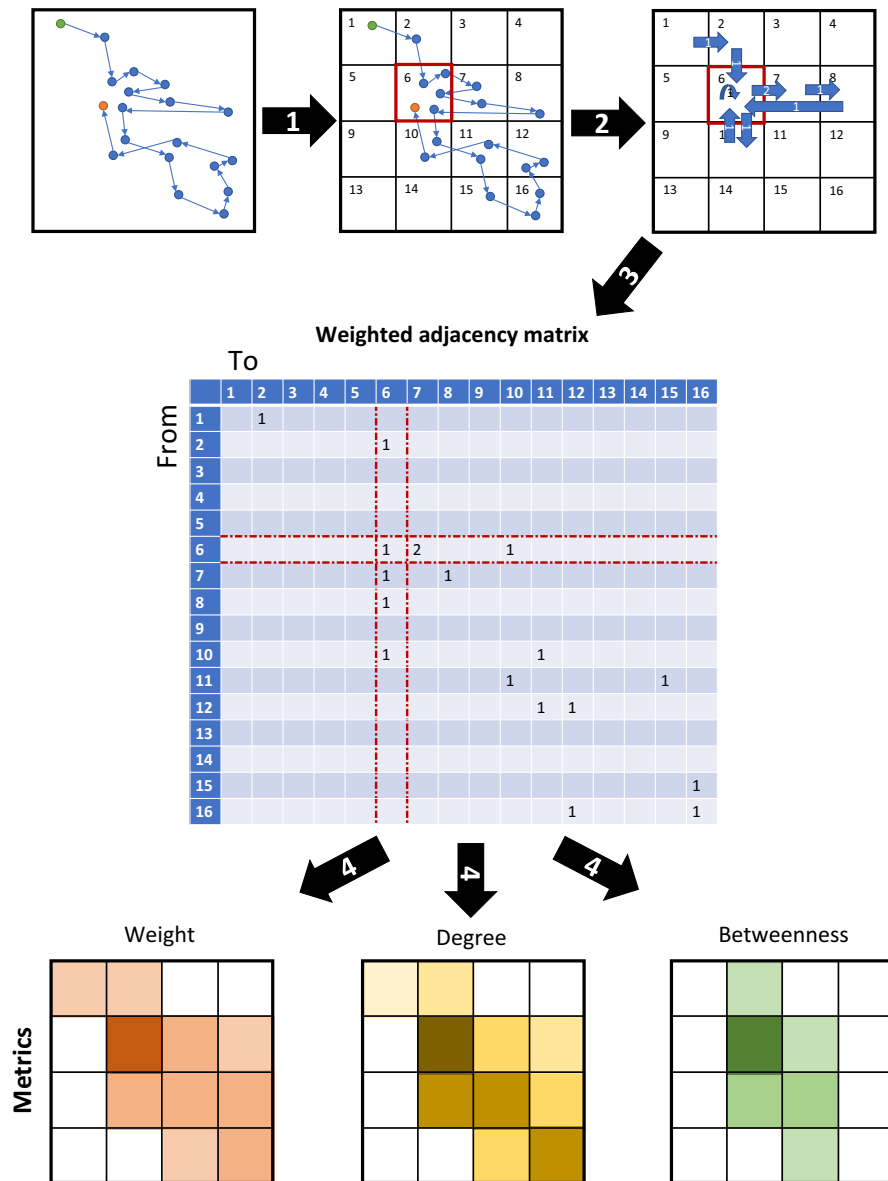


FIG. 1. Pathways illustrating how network metrics can be estimated directly from relocation data. First a grid is overlaid with relocation data (arrow 1). From this grid, the number of connections from and to each pixel is summed (arrow 2) and entered in a weighted adjacency matrix (arrow 3). From this adjacency matrix, multiple network metrics can be calculated and displayed as a raster (arrows 4).

Node-level metrics and local space-use

The definition of local spatial properties is a critical objective in movement ecology. We explored the effectiveness and utility of six different metrics (weight, self-loop number, degree centrality, betweenness, clustering coefficient, and eccentricity; Table 1) for defining core space use and critical areas for interpatch movement (connectivity) in simulated movement trajectories representing movement among multiple patches. Movement was simulated using a two-dimensional Ornstein-Uhlenbeck process for movement within a core range and a Brownian bridge motion model for movement between patches, randomly moving to an alternative patch during transitions. These simulations corresponded to the migratory and multi-patches movement

explained in the “Graph-level metrics and characterization of large-scale movement patterns” section. Code for movement strategy simulations is provided in Data S1.

In addition to assessing the ability of network metrics to define known features, we tested the sensitivity of metrics to movement and grid properties including (1) the grid size used to construct the network, (2) the number of patches in the network, (3) the ratio of locations associated with patches and interpatch movement, (4) the sampling interval, and (5) the discreteness of patches and corridors. For all simulation scenarios, we generated 1,000 movement trajectories for each iteration of parameters (i.e., $n = 4,000$ for each set of scenarios [row] in Table 2). We calculated each metric, which was then used as a response variable in a Gaussian mixture model with unequal variance to cluster values in

TABLE 1. Network metrics extracted from relocation data.

Metric	Definition
Node-level metrics	
Weight	number of locations within a pixel
Self-loop	sum of sequential relocations in the same pixel
Degree centrality	number of different pixels a pixel is connected to
Betweenness centrality	number of shortest paths going through a pixel relative to the total number of shortest path (the importance of a pixel in the organization of flows in the network)
Eccentricity	distance of a pixel to farthest other pixel in the graph
Clustering coefficient	probability that the adjacent pixels are connected
Graph-level metrics	
Diameter	maximum length (or maximum eccentricity) of the network
Clustering coefficient	degree to which nodes tend to cluster together
Density	ratio of the number of edges vs. the number of potential edges
Modularity	represents the level of sub clustering in graph

two groups potentially representing patches and interpatch movement. We then evaluated the error of commission (percentage of simulation improperly assigned to a cluster or false positive), error of omission (percentage of simulation not assigned to the appropriate cluster or false negative), and Cohen’s kappa statistics (overall accuracy; Cohen 1960) when comparing the cluster defined groupings to the known, simulated conditions to quantify the efficacy of a given metric under known circumstances to capture core areas and interpatch movement (average values as well as 95% quantile confidence intervals reported in Appendix S1). Lastly, we calculated these different node-level metrics for an individual elephant, giant tortoise, and mule deer using a grid size representing the median step length of this individual (see section “Graph-level metrics and characterization of large-scale movement patterns” for details about each data set).

Graph-level metrics and characterization of large-scale movement patterns

A fundamental question in movement ecology is the type of movement pattern demonstrated by a species, commonly grouped into broad categories of nomadic, migratory, or range resident. We explored the use of graph-level metrics to

distinguish between movement strategies by applying graph theoretic analyses to simulated movements representing four, simplified and stereotypical movement strategies (migration, structured multi-patch movements, residency, and nomadism). Migration was simulated using a two-dimensional Ornstein-Uhlenbeck process for movement within a core range and a Brownian bridge motion model for migratory movement between two patches, where the ratio of locations associated with the core range vs. migratory journey was adjusted. Multi-patch movements were simulated using a similar model structure, but with three to five core areas (patches) instead of two, for which individuals randomly moved to an alternative patch during transitions. Range residency was simulated using a two-dimensional Ornstein-Uhlenbeck process, for which heterogeneity in the movement was elicited by defining 10 closely located attraction centers that animals randomly switched between. The attraction and noise parameters were adjusted so that movement around each center overlapped. Last, we simulated nomadic movement using a random walk model, with no bounds. Code for movement strategy simulations is provided in Data S1.

For each of the four simulated movement categories we extracted and compared graph-level metrics including diameter, clustering coefficient, density, and modularity. To better understand potential underlying relationships between these graph-level metrics and properties associated with simulated movement strategies, we performed a principal component analysis (PCA) to identify the primary, uncorrelated components for each movement strategy. In addition, we calculated the graph-level metrics using the median step length of each individual as the grid size for 58 individual elephants, 40 giant tortoises, and 75 mule deer that were followed for at least one year to assess how variation in network metrics in real systems corresponded to the variation initially observed within our simulations from the PCA first two-axes. Relocations fix frequency was 30 min for mule deer, 1 h for giant tortoises, and 2 h for elephants (some elephants were sampled at different frequency and were all resampled to 2 h). All data were preprocessed so that missing locations were identified within the time series of GPS locations (i.e., observed steps were part of a regular trajectory). Further details about each data set are provided in Wittemyer et al. (2017), Bastille-Rousseau et al. (2017a), and Northrup et al. (2016), respectively. All analyses were done in R 3.3.2 using the packages adehabitatLT (Calenge 2006), igraph (Csardi and Nepusz 2006), mclust (Fraley and Raftery 2002), raster (Hijmans 2016), fmsb (Nakazawa 2015), and ggplot2 (Wickham 2009). We also implemented functions to perform the analyses

TABLE 2. Simulation scenarios testing the effectiveness of different node-level network metrics in capturing local movement properties.

Scenarios	Grid size (percentile of step length distribution)	Number of simulated patches	Ratio of location in patch vs. corridor (%)	Location sampling time interval	Minimum distance between patches (discreteness)
Grid size	25, 50, 75, 90	4	95	1	200
Number of simulated patches	50	2,3,4,5	95	1	200
Patch/corridor location ratio	50	4	50, 65, 80, 95	1	200
Location sampling interval	50	4	95	1, 2, 10, 25†	200
Distance between patches	50	4	95	1	200, 100, 50, 25

†E.g., a time interval of 25 means that the data are sampled every 25 time steps instead of every step.

TABLE 3. Descriptive summary of the performance of different metrics in classifying core areas and corridors.

Metrics	Limitations	Preferred when
Degree	grid size becomes too big, decrease in patch discreteness, low sampling intervals, patches/corridors ratio close to one	grid relatively fine scaled, high-resolution sampling, strong spatial structuring
Weight	same as specified for degree	same as for degree
Betweenness	relatively high omission error rates	low discreteness or overlap between patches
Eccentricity	perform poorly except for migratory movement	migratory movement (two patches), ratio of patches/corridors location close to one
Clustering coefficient	low classification success in all instances	never
Self-loop	low classification success in all instances	never

Notes: Summary is based on scenarios presented in Table 2 and kappa statistics and errors of commission and omission presented in Appendix S1: Table S1. Metrics are presented in order of versatility and performance.

mentioned above in the R package *moveNT* (*available online*).⁸ We provide step-by-step illustration of how to use the package in Appendix S2.

RESULTS

Node-level metrics and local space use

Assessment of the efficacy of node-level metrics to capture local space use properties in simulated movement trajectories revealed the general utility of several metrics, particularly to define core areas and interpatch movements (corridors). Degree has the highest kappa statistic relative to other metrics for defining patch and corridor areas (Appendix S1: Table S1). The performance of degree, however, was somewhat sensitive to grid properties. The kappa statistics of degree were highest when using a grid size representing the median or 75th percentile of distance travelled (Appendix S1: Table S1). Results for weight generally were parallel to degree (it was only slightly less accurate when relocation data were sparse). Betweenness had the lowest rate of commission error for corridor definition and performance increased when the ratio of patch/corridor locations approached one and the discreteness between patches decreased (Table 3). When patches were not discrete, betweenness outperformed degree, particularly for classifying patches (Appendix S1: Table S1) potentially indicating the usefulness of betweenness when applied to more complex movement data (Table 3). However, betweenness had lower kappa scores relative to degree and weight for characterizing patch and corridors. Relative to other metrics, clustering coefficient and self-loop number performed poorly in classifying patch and corridor (Table 3), but highlighted other attributes of potential interest. Eccentricity outperformed degree in classifying corridors and patches when the ratio of the location between patches and the corridor was close to 50%, but was generally less accurate given other data structures (Table 3).

Node-level metrics applied to elephant, tortoise, and mule deer relocation data confirmed the potential of network metrics to identify key local properties of animal movement (Appendix S1: Table S2). Parallel to findings from simulated data, weight and degree highlighted areas of intensive use for all species (Figs. 2–4). Similarly, betweenness captured the migratory journey for tortoise and highlighted corridors

in elephant movement (Figs. 2–4). Eccentricity performed well at classifying patches in simulated migratory movements, whereas it performed poorly on tortoises data, most likely because the examined tortoise migratory routes did not overlap (Appendix S1: Figs. S1–S3).

Graph-level metrics and characterization of large-scale movement patterns

Graph-level metrics were differentiated across the simulated movement strategies, with the two principal components (PC) of the PCA explaining 94% of the variance among the graph-level metrics (only the first axis was retained using the Broken-stick criterion). PC1 was associated more strongly with the clustering coefficient, density, and diameter (Fig. 5). PC2 was more strongly associated with modularity (Fig. 5). PC1 disentangled nomadic movements from other strategies with purely nomadic movements generally having higher clustering coefficient and density than other strategies (Fig. 5). PC2 distinguished range residency (or sedentarism) from structured movement. Range residency generally had higher modularity. Migration and multiple patch movements had higher diameter, lower density, and lower clustering coefficient (Fig. 5).

Projecting metrics from true movements of elephant, mule deer, and tortoise onto the PCA scatterplot revealed that most individuals of each species fell in the middle of the PCA projected space with limited overlap of regions associated with a given strategy (Fig. 6). This would suggest intermediate strategies relative to the strict simulated movements, although most individuals were in proximity to the cluster indicative of a specific strategy. Movements of elephants and tortoises were assigned near the vertices representing simulated nomadic strategists and migratory/multi-patch movements, with most of the variation in their movement explained by PC1. In contrast, the more simplistic movements of mule deer were found between resident and migratory/multiple-patch movements, with variation explained by PC2 (Fig. 6).

DISCUSSION

Our analytical framework provides a straightforward approach to apply network theory to animal relocation data, providing both graph- and node-level metrics to describe multi-scale patterns of animal movement at the local (patch) and system-wide (individual animal range or

⁸ <http://github.com/BastilleRousseau/moveNT>

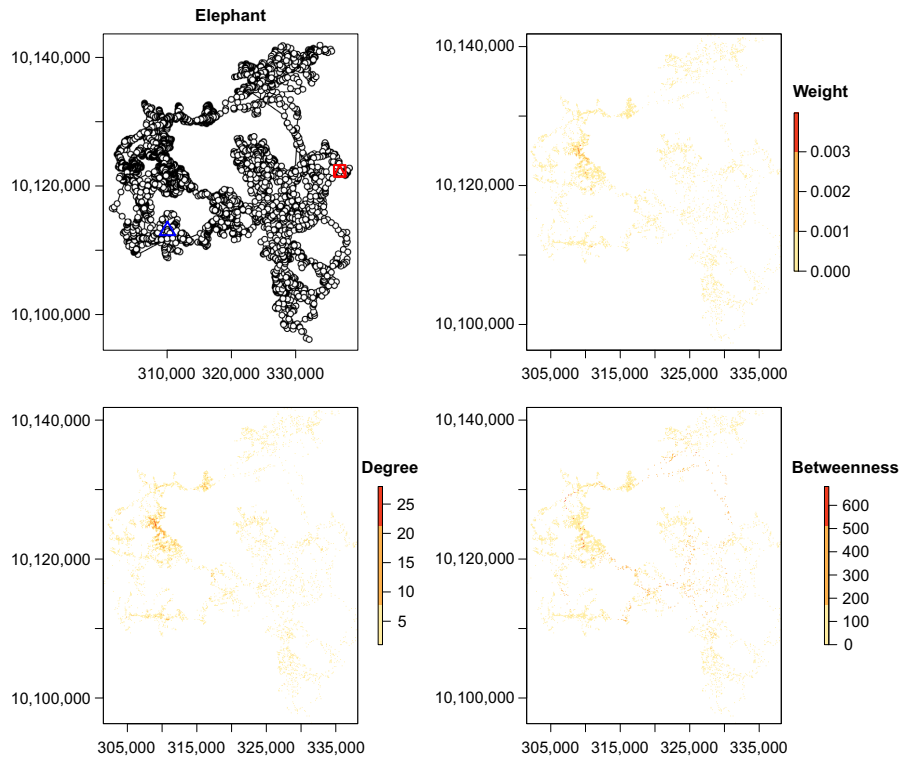


FIG. 2. Node-level network metrics calculated on African elephant movements. Upper left panel represents the actual movement trajectory with the first and last locations represented by the blue triangle and red square, respectively. Pixel size (115 m) is based on the median step length for the individual. Additional metrics are presented in Appendix S2.

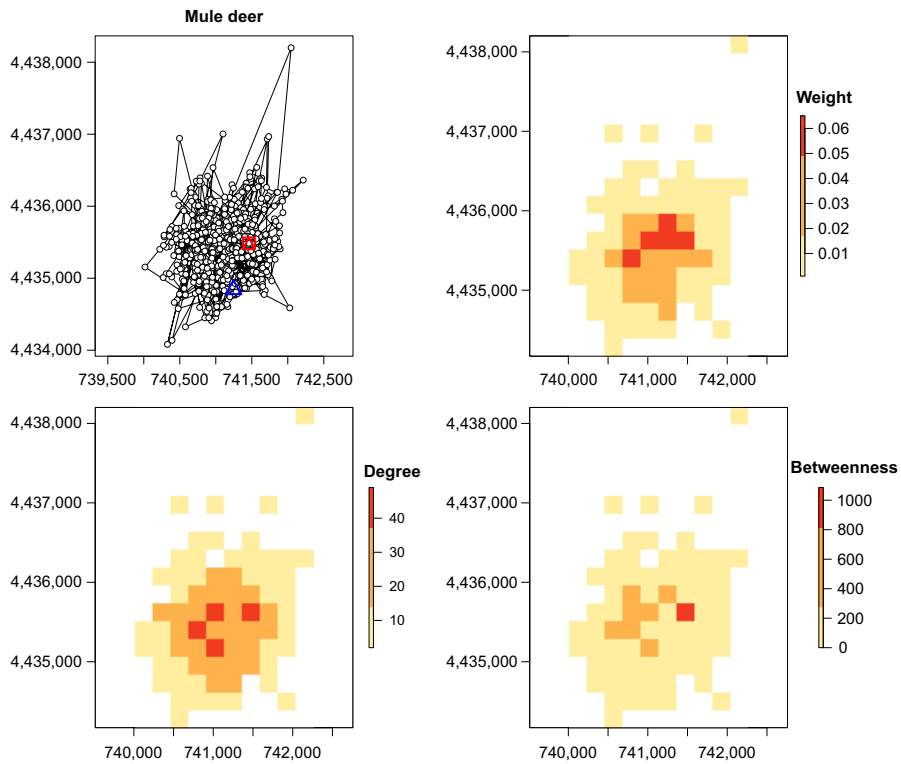


FIG. 3. Node-level network metrics calculated on mule deer movements. Upper left panel represents the actual movement trajectory with the first and last locations represented by the blue triangle and red square, respectively. Pixel size (223 m) is based on the median step length for the individual. Additional metrics are presented in Appendix S2.

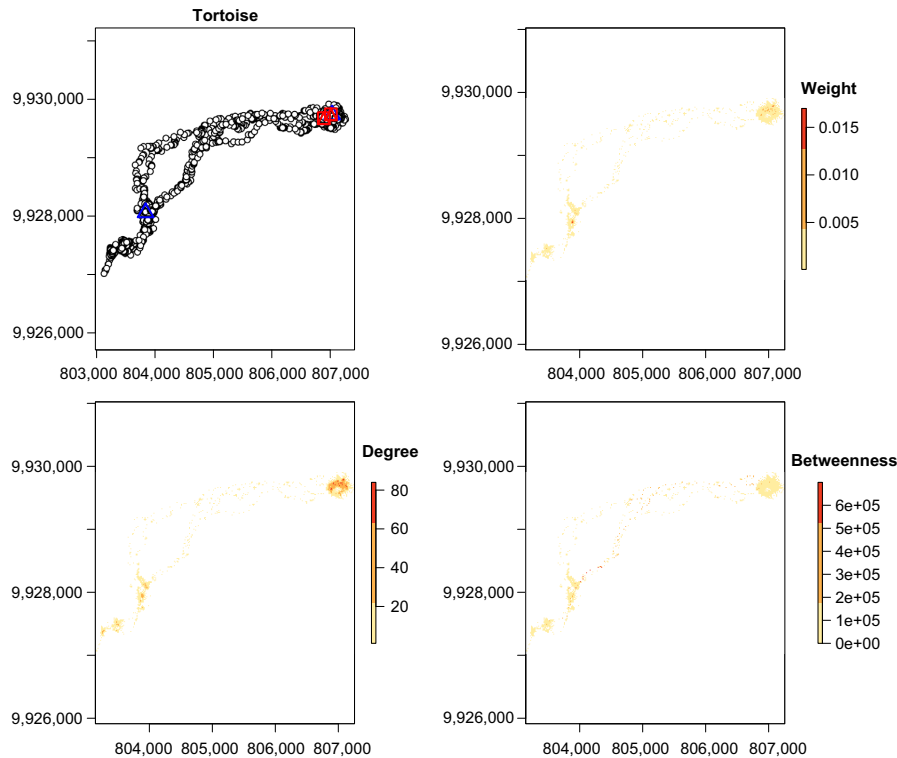


FIG. 4. Node-level network metrics calculated on Galapagos giant tortoise movements. Upper left panel represents the actual movement trajectory with the first and last locations of a movement bout represented by the blue triangle and red square, respectively. Pixel size (15 m) is based on the median step length for the individual. Additional metrics are presented in Appendix S2.

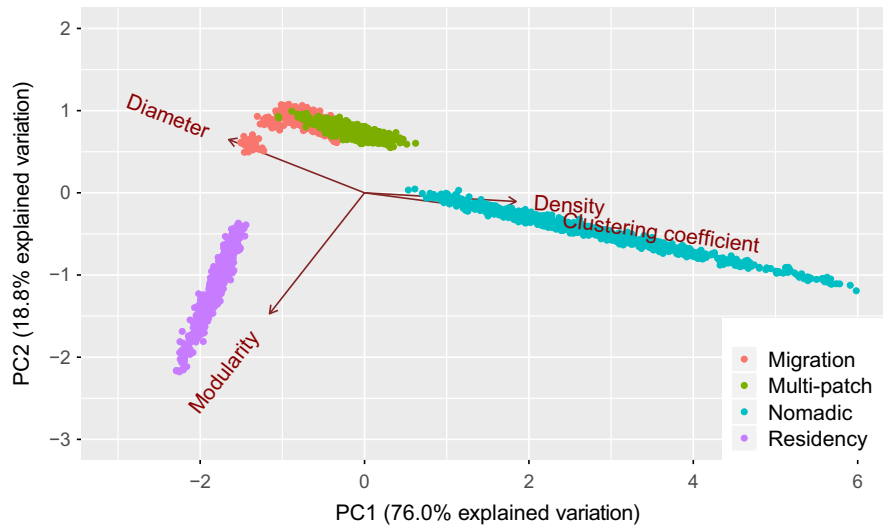


FIG. 5. Scatterplot of simulated movement strategies based on PCA-defined axes. PCA was based on graph-level metrics (modularity, density, clustering coefficient, and diameter).

study area) level. Collectively, these metrics provide exciting new avenues for exploring and quantifying animal movements. The node-level metrics degree centrality and weight effectively defined simulated core areas and areas associated with inter-patch movement, irrespective of assumptions structuring analysis or strategies of movements. Betweenness was accurate at identifying areas of importance for connectivity, particularly for empirical movement

collected on elephants, mule deer, and tortoises, which employ starkly different movement strategies. However, betweenness was more sensitive to data structure than degree or weight in analyses of simulated data sets. Other node-level metrics showed context-specific utility for identifying interesting structural points in movement data. Our analysis indicated that graph-level network metrics are unlikely to be as informative as other alternatives (e.g., net

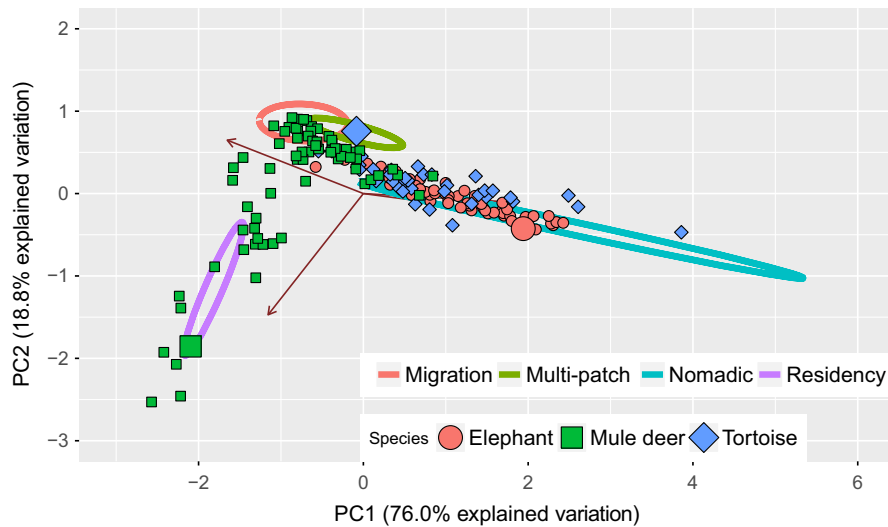


FIG. 6. Scatterplot of elephant, mule deer and tortoise movement characteristics overlaid on PCA-defined axes (see Fig. 5). Ellipses represent the 68% (1 SD) contour of simulated movement strategies. Individuals represented in Figs. 2–4 are also indicated on the figure using bigger symbols.

squared displacement) to characterize stereotypical movement strategies.

Using network metrics to characterize local space-use differs from other, frequently employed approaches that focus on movement properties (i.e., speed and directionality) to identify movement states. Such analyses often use behavioral change point analysis or hidden Markov models (Morales et al. 2004, Patterson et al. 2008, Gurarie et al. 2009) to delineate behavioral modes in recorded movements. Though powerful, these approaches tend to be sensitive to data sampling issues. For example, the graph theoretic approach we employed does not assume any parametric changes in step length and/or turning angle distributions, which are also a function of sampling frequency (Fleming et al. 2014, Bastille-Rousseau et al. 2017b), but instead, examines patterns in transitions among locations. This difference in approaches may facilitate application to a wider range of species and data sets (i.e., with lower resolution of sampling or sporadically sampled movement processes). Our framework also differs from other methods in that it leads to spatial predictions that are generalized over multiple relocations (i.e., metrics are calculated over a grid; Fig. 1). Overall, our examination demonstrated that graph theoretic approaches provide an intuitive and straightforward way to analyze relocation data, offering a powerful analytical framework to assess functional movement properties.

Node- and network-level metrics

Given the broad interest in using movement data to identify local movement patterns including core areas of use and interpatch movements, we found weight, degree, and betweenness effectively identified locations with important structural properties valued in applied movement studies (Table 1). In most instances, degree or weight metrics demonstrated substantial agreement with simulated patches and interpatch movements (Appendix S1: Table S1). Whereas properties captured by weight are analogous to other approaches characterizing

intensity of use, such as using kernel density estimator with low isopleth values or time spent in a vicinity (Barraquand and Benhamou 2008, Wall et al. 2014), degree captures unique properties for core area definition. Degree is not just a function of the proportion of time spent in a given area, but considers how frequently animals are transitioning to and from this area, akin to central-place foraging. Degree and weight captured different processes indicative of restricted space use, though they were similar in terms of the ability to identify core areas in our simulations. This means that the appropriate choice among metrics may differ according to the foraging strategies of the animal (Bastille-Rousseau et al. 2010, Abrahms et al. 2017). Betweenness performed relatively poorly in classifying simulated core areas, but was more effective at identifying interpatch movements and appeared to work well in identifying key connectivity passages on empirical data sets. Eccentricity performed well in identifying core areas as well as migratory routes of simulated migration, but did not appear to perform well when applied to empirical data of individuals that demonstrated little adherence to specific migratory routes (e.g., giant tortoise example; Fig. 4). The self-loop metric highlighted locations where individuals remained for extended periods, but this property did not reflect core areas or corridors. Applying this metric to networks where the grid size is significantly smaller than the median step length will provide insight to repeated use locations, potentially related to rest or cover (Wittemyer et al. 2017), or areas of high forage density.

The identification or classification of species' general movement strategies has been a goal of movement ecology method development and analysis for some time (Bastille-Rousseau et al. 2016). Simulated movement associated with different strategies (e.g., sedentary, nomadic, migratory, and multi-patches) showed distinct clusters based on their graph-level metrics (Fig. 5), suggesting broad-scale network-level metrics may be effective for categorizing broad categories of movement strategies. However, extracting the same graph-level metrics from animal relocation data illustrated that the

initial separation observed among strategies was not as apparent when applied to empirical data (Fig. 6). This was particularly evident with giant tortoises where clear patterns of partial migration have been documented previously using net squared displacement (Bastille-Rousseau et al. 2017a), yet very few individuals were found in the PCA space associated with migratory or resident individuals (Fig. 6). Speculatively, these differences are likely a function of nonstationary processes in actual animal movement data not captured in simulated data. As such, our approach is unlikely to become an alternative to existing approaches that classify movement strategies, such as the ones based on net squared displacement (Bastille-Rousseau et al. 2016, Cagnacci et al. 2016, Spitz et al. 2016). Rather, graph-level metrics are more likely to clarify individual differences in movement within group, population, or species.

Consideration when applying graph theoretic approaches to real data

We demonstrated the utility of graph theoretic approaches for understanding local space use properties, information that can be valuable to local area management and conservation planning. Whereas general patterns in graph-level metrics among individuals can be assessed using a PCA or multivariate clustering, we recommend focusing analysis on local area properties. Approaches relying on the grouping of node-level metrics using a clustering approach such as normal mixture modeling (Fraley and Raftery 2002) or identifying nodes that deviate from given quantiles/percentiles for specific metrics can highlight locations of interest, particularly in respect to delineating core areas or locations important for connectivity. Alternatively, comparing node-level metrics calculated from empirical movements to those generated from random walk models or randomization of the adjacency matrix can identify salient features in the graph (Psorakis et al. 2012, Farine 2013). Due to the intuitive nature of graph theory, we believe that use as a visualization and exploratory tool can be particularly illuminating regarding local space-use properties. We did not explore time-ordered network properties, but detection and occurrence of motifs in movement networks may be useful to unveiling spatiotemporal patterns in animal movement (Jacoby and Freeman 2016).

Outputs from this approach (and most others) is subject to relocation sampling frequency and applied network grid size, which can influence outputs. Our sensitivity analysis showed that metrics were relatively stable across a wide range of grid sizes (25% to 75% quantile of step length). Intuitively, using the median step length as the default grid size is biologically logical. Sensitivity analyses demonstrated that reducing the frequency of relocations affects metrics. Given the ability of the approach to process large amounts of data, we recommend that users err on the side of using finer scale relocation, while keeping in mind the biological process of interest. Since the representation of an animal movement network improves with tracking duration, we also recommend applying the analysis over the entire data set. Analyzing data by seasons and/or year can provide insights to changes in space use, but at the cost of information on the broader network. The approach is flexible

enough to handle missing locations in relocation data when all steps have the same time interval.

To facilitate the use of network theoretic approaches in movement ecology, the functions we employed have been collated and made available within the package *moveNT* and with an accompanying vignette (also presented in Appendix S2). This package makes use of functions and object classes available from popular R packages (e.g., *raster*, *igraph*, and *adehabitatLT*). The framework is not resource intensive and therefore fast and can be easily applied to data set including $>10^6$ locations from over 150 individuals using consumer-level computers and in less than one hour. The functions are designed to be applied at the individual level, but a raster of node-level metrics can be easily mosaicked (i.e., stacked and averaged) together to obtain population-level inferences, while also allowing maximum flexibility to the user. Whereas we constructed weighted networks and applied metrics that did not require information on direction, using an unweighted network may be preferred for studies focusing on the spatial configuration rather than intensity of use in the movement network. Greater exploration of approaches using directed networks is merited, particularly where patterned space use is suspected.

Spatial delineation of areas with different use properties and significance in terms of connectivity is critical in mitigating the impact of landscape alteration on animal movement. Our approach provides a useful way to define core use areas and areas of high importance for connectivity, and offers a quick and quantifiable means to evaluate the impacts of removing specific nodes on connectivity. For example, our approach can identify if access to areas of interest will be compromised when specific nodes are removed. Previous alternative approaches that do not use movement data are prone to greater assumptions in their assessments of potential use and connectivity (LaPoint et al. 2013), which may lead to erroneous identification or prioritization. In contrast, our approach provides insight into functional connectivity given that it is based off empirical relocation data, but inferences are limited to areas where animals have travelled. Our framework is a useful addition to the toolbox of movement ecologists, landscape ecologists, and wildlife managers.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.1697/full>

DATA AVAILABILITY

Functions and associated documentation are available within the R package *wildxing*: <https://doi.org/10.5281/zenodo.1162358>.
Data sets are available on FigShare: <https://doi.org/10.6084/m9.figshare.5821194>.